OENOTHERA BRANDEGEEI FROM BAJA CALIFORNIA, MEXICO, AND A REVIEW OF SUBGENUS PACHYLOPHUS (ONAGRACEAE)

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In December 1887, while collecting for the Smithsonian Institution, Edward Palmer made two collections of an interesting annual *Oenothera* on stony ridges near Bahía de los Angeles on the east coast of Baja California (*542,* GH, and *582,* US). These collections, each of a single plant, were determined by Sereno Watson as *O. caespitosa* Nutt. They remained under this name until 1930, when they were studied by P. A. Munz (1931) for his revision of *Oenothera* subg. *Pachylophus*. Munz considered them a distinctive unnamed variety of *O. caespitosa* which he named var. *brandegeei* Munz (1931), selecting no. *542* as the holotype. Munz assumed this plant to be the same as the one mentioned by T. S. Brandegee (1889) as "*Oenothera caespitosa* Nutt. var. Leaves finely divided and villous.—El Campo Aleman"; but Brandegee's specimen (El Pozo Alemán, 23 April 1889, UC) had long since been determined by Katherine Brandegee as *O. primiveris* Gray, and Munz himself concurred when he examined the specimen in 1932. In 1965, treating the Onagraceae for the North American Flora Munz raised this rare and local endemic to the rank of subspecies as *O. caespitosa* Nutt. ssp. *brandegeei* (Munz) Munz. Until 1966, Palmer's two plants remained the only known representatives of *O. caespitosa* var. *brandegeei.*

Recently, Reid Moran very kindly sent me a collection he had obtained 22 April 1966 on Isla Angel de la Guarda in the Gulf of California. The plants grew among volcanic rocks on the north slope of the peak southwest of Pond Island, ca. 350 m elevation, near 29°01′N, 113°10′W, *12983* (DS, RSA, SD). Moran found occasional woody dead plants from earlier years' growth with the capsules adhering, and also a few dozen living ones with leaves mostly 3–4 cm long and one capsule per plant (Palmer's had leaves respectively ca. 8 and ca. 15 cm long). In these depauperate plants, the terminal lobes of the leaves are less prominent than in Palmer's collections, and the flowers are smaller: hypanthium 5 mm. long, sepals 5 × 0.7 mm, petals about 8 × 4.5 mm, filaments 5 mm long, anthers about 3 mm long in Moran's material, and respectively 38 mm, 12 × 3 mm, 16 × 15 mm, 7 mm. and 5 mm in Palmer's *582*. In every other way, however, Moran's plants are identical with Palmer's, and there is no doubt that all three represent the same entity. The dead plants of earlier years that Moran collected were much more robust, with about 30 capsules per plant.

When I examined Moran's material, it became clear to me that these slender annuals of Baja California should not be considered conspecific

with *O. caespitosa* Nutt., itself an exceedingly polymorphic species, but a robust, tufted perennial with much larger flowers. *O. caespitosa* is basically a species of the Great Basin of the western United States, extending south to the San Bernardino Mts. of southern California and the Huachuca Mts. of southeastern Arizona, but not known from Mexico. *Oenothera caespitosa* is, as far as is known, always self-incompatible (Gregory, 1963; Klein, pers. comm.) whereas "var. *brandegeei,*" with its small flowers and stigma surrounded by the shedding anthers at anthesis, is highly autogamous as shown by three plants grown at Stanford from Moran's collection. The change from self-incompatibility to autogamy is known often to accompany a change from the perennial to the annual habit in angiosperms.

This discussion to this point establishes the desirability of separating "var. *brandegeei*" from *O. caespitosa* at the specific level. There is, however, another basically annual species with small white flowers which is closely related to *O. caespitosa,* namely *O. cavernae* Munz (1941). *Oenothera cavernae* is so similar to "var. *brandegeei*" that Munz annotated a specimen of the former ("Utah, Capt. Bishop, 1872," US) as follows: "*Oenothera caespitosa* var. *brandegeei* . . . This is a plant from Lower California. The data on the label certainly incorrect. PAM—1930." This was, of course, before Munz was aware of the existence of *O. cavernae* as a distinct entity. Despite their overall similarity, there are a few differences which clearly distinguish *O. cavernae* from "var. *brandegeei.*" As pointed out by Munz, the leaves of "var. *brandegeei*" are distinctive in the *O. casespitosa* alliance in being deeply divided into narrow, acuminate, lobes which are directed forward, toward the apex of the leaf. These lobes are much reduced, and the treminal lobe is very prominent in well-developed individuals. In *O. cavernae,* on the other hand, as is usually the case in *O. caespitosa,* the lateral lobes are acute or obtuse and stand out at right angles to the rachis. The terminal lobe of the leaf is much less prominent than in "var. *brandegeei.*" The capsules of the two entities likewise differ modally, those of var. *brandegeei*" being short and stout, 14–18 mm. long, with very prominent, well separated tubercles along the lines of dehiscence; whereas those of *O. cavernae* are often longer, 15–38 mm long, with an acuminate apex and less prominent or distinct tubercles.

In summary, their morphological distinctiveness and wide geographical separation suggests that these two white-flowered, autogamous annual species were derived independently from *O. caespitosa* as the deserts of western North America expanded and the available habitats became progressively less favorable for their perennial ancestor. The distinctive leaves of "var. *brandegeei*" suggest that it may have been the earlier derivative, an hypothesis consistent with its present geographical separation from *O. caespitosa. Oenothera cavernae* occurs on the desert slopes of southern Nevada (Clark Co.) and southeastward to Toroweap and

Havasu Canyon on the Colorado River in northwestern Arizona. *O. caespitosa* occurs at higher elevations and presumably in more mesic sites, often associated with juniper woodland and sometimes with pinyons, in the same region. In view of these considerations, a new combination seems appropriate.

Oenothera **brandegeei** (Munz) Raven, comb. nov. *O. caespitosa* Nutt. var. *brandegeei* Munz, Amer. J. Bot. 18:732. 1931; *O. caespitosa* ssp. *brandegeei* (Munz) Munz, N. Amer. Fl. II. 5:101. 1965.

As I have earlier pointed out the importance of a modern and comprehensive reevaluation of sectional and subgeneric alignments in *Oenothera* (Raven, 1964), it may be appropriate at this point to offer a few comments concerning the relationships of the six species currently referred to subg. (sec.) *Pachylophus* and the overall constitution of the group. First, it is clear that *O. caespitosa, O. cavernae,* and *O. brandegeei* form a close-knit alliance. In the protologue of *O. cavernae,* Munz compared it with the yellow-flowered desert annual *O. primiveris* Gray, but these two species do not appear to be closely related. On the other hand, the annual *O. primiveris* does appear to be related to the yellow-flowered perennial *O. xylocarpa* Cov., a narrow endemic found along the east flank of the southern Sierra Nevada in California and Nevada. Unlike *O. caespitosa, O. xylocarpa* has swollen, fleshy underground parts. In this, as in the morphology of the capsule, it closely resembles the sixth species of the group, the white-flowered (not yellow, contrary to the prediction of Munz (1931; 1965), *O. tubifera* Sessé & Mocino ex Ser. of central Mexico.

Oenothera tubifera in turn is obviously closely related to another white-flowered perennial Mexican species currently referred to subg. *Raimannia*: *O. muelleri* Munz. Although the flowers of *O. muelleri* are much larger, these two species can be crossed easily in cultivation, and the seeds germinate readily to produce healthy F_1 individuals. These two species are identical in capsule morphology and in habit, the plants producing a series of decumbent flowering branches from a central rosette.

Another Mexican species currently referred to subg. *Raimannia, O. macrosceles* Gray, is similar in habit, but has yellow flowers and much more slender capsules. It is clearly not as closely related to *O. muelleri* and *O. tubifera* as they are to one another. *Oenothera macrosceles* can easily be hybridized with *O. muelleri* and *O. tubifera* in cultivation, however, but we have not yet succeeded in germinating the seeds. On the other hand, Cleland (1968) has recently shown that *O. macrosceles* does not hybridize readily with any species of *Raimannia*. On the balance, it would seem that *O. macrosceles* should be placed in subg. *Pachylophus*.

Although the yellow-flowered *O. maysillesii* Munz of Durango, Mexico, is similar in habit and has been compared with *O. muelleri* and *O. macrosceles,* its status is currently being investigated, and it is best retained

at least for the time being, in subg. *Raimannia,* as originally placed.

Oenothera subg. *Raimannia* (revised by Munz, 1935) is a relatively homogeneous group in South America, but has been made to include a much more diverse assemblage of North American species. *Oenothera macrosceles* and *O. muelleri,* as suggested above, seem best referred to subg. *Pachylophus,* and *O. albicaulis* Pursh and *O. coronopifolia* T. & G. are best romoved to a ditypic group of their own—sect. *Kleinia* Munz (1965), perhaps best thought of as intermediate between subg. *Raimannia* and subg. *Anogra. Oenothera organensis* is now regarded as belonging to a monotypic sect. *Emersonia* (Munz, 1965) perhaps intermediate to subg. *Oenothera* (*Euoenothera*). With these subtractions, subg. (sect.) *Raimannia* appears to be a reasonably natural group, although rich in species. Interestingly, all of the remaining species would have yellow flowers.

These rearrangements would leave *Oenothera* subg. *Pachylophus* with a total of eight species, with *O. macrosceles* and *O. xylocarpa* yellow-flowered perennials, *O. primiveris* a yellow-flowered annual, *O. tubifera, O. muelleri,* and *O. caespitosa* white-flowered perennials, and *O. brandegeei* and *O. cavernae* white-flowered annuals. Relationships within this group need further clarification by biosystematic studies, but it appears at present that *O. caespitosa, O. cavernae,* and *O. brandegeei*; *O. xylocarpa* and *O. primiveris* (which have been hybridized experimentally, although the seeds could not be germinated; Klein, pers. comm.); *O. macrosceles*; and *O. muelleri* and *O. tubifera* constitute four distinct subgroups. Three species, *O. caespitosa, O. xylocarpa,* and *O. primiveris,* are self-incompatible (Klein, pers. comm.); two, *O. muelleri* and *O. macrosceles,* are self-compatible but modally outcrossing; and two, *O. brandegeei* and *O. cavernae,* are autogamous. In *Oenothera tubifera,* self-pollination is frequent but since a relatively small load of pollen is deposited on the stigma, full seed set does not normally result.

Oenothera subg. *Pachylophus* as constituted here appears to include an assemblage of relatively closely related species, and to embody a useful taxonomic concept. The four groups mentioned above might reasonably be regarded as distinct sectioins, but further studies of the entire genus will be necessary to determine the best systematic treatment for the group as a whole. It might be noted in closing that *O. caespitosa* and *O. primiveris* include several distinct races best recognized at the subspecific level, but the other species appear relatively homogeneous.

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POLLEN APERTURE VARIATION AND PHYLOGENY IN DICENTRA (FUMARIACEAE)

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Dicentra Bernh., comprising some 20 species of perennial and biennial herbs and climbers of North American and East Asian distribution, was monographed by Hutchinson (1921) as part of a larger treatment. Fedde (1936) largely followed Hutchinson's treatment in his discussion of the Papaveraceae, although both earlier works were incomplete. In my revision of the genus (1961; 1967), phylogenetic trends, based primarily on morphological and anatomical features, were discussed. Berg (1964), studying seed dispersal ecology in *Dicentra* independently, reached essentially similar conclusions about the intrageneric phylogeny, as did Fahselt and Ownbey (1968) while investigating the flavonoid components. Cytological evidence obtained by Ryberg (1960), Ernst (1965), Stern (1968) and others suggests the development of a polyploid series accompanying morphological and chemical advancement, but further extensive study is needed before the role of polyploidy in the evolution of the genus, and cytotaxonomic interrelationships in general can be clearly portrayed.

After brief mention of pollen morphology in my 1961 monograph, I studied *Dicentra* pollen grains in more detail (Stern, 1962), and found the interspecific variation not only extensive, but specifically constant enough to permit distinguishing between all except two of the species on the basis of pollen morphology alone. Such interspecific variation is exceptional, although not wholly unique, as the representative studies of Dahl (1952), Fasbender (1959), Helmich (1963) and Lewis (1965) suggest. My 1962 study included descriptions and dimensions of the pollen grains and mention of phylogenetic trends. This study amplifies